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CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS. II

DR. F. B. SUMNER

SCRIPPS INSTITUTION, LA JOLLA, CALIF.

IV. HEREDITY OF THE RACIAL DIFFERENCES

In view of the long-recognized correlation between certain of these subspecific characters—namely, those relating to pigmentation—and certain factors of the physical environment, the possibility has suggested itself that the characters in question might be purely "ontogenetic," *i. e.*, produced anew in each generation by the action of external physical factors. The simple experiment of transplanting mice from one habitat to another has disposed of this suggestion.

As I have more than once reported elsewhere (1915*a*, 1917, 1917*b*) entirely negative results have been reached, so far as climatic influences are concerned. Neither the transference of the desert race to Berkeley, nor the transference of both the desert and the redwood races to La Jolla have resulted in any demonstrable change, at least up to the third cage-born ("C_3") generation.

The La Jolla test is the more satisfactory of the two, since the number of animals employed is very much greater. Thus far, however, only the C_2 animals (38 *rubidus* and 96 *sonoriensis*) have been killed, measured and (in part) skinned. The C_3 generation is still kept alive for breeding purposes, but the characteristic racial differences are obvious. On comparing the skins of the palest and the darkest *rubidus*, or the palest and darkest *sonoriensis* of the C_2 generation, with the extremes among the wild grandparents, it will be seen that the range of color variation has not appreciably changed.

Not only are the larger color differences which distinguish these main races heritable, but certain lesser differences which distinguish narrowly localized sub-races have been shown to be genetic characters. In a recent paper (1917) I discussed an aberrant colony of "*rubidus*" inhabiting an isolated sand-spit fronting on the ocean.[15] The evidence for the inheritance of these peculiarities of color may now be stated somewhat more strongly than was done in that paper. Upon preparing the skins of the three C_1 members of this sub-race, born and reared at La Jolla, it was found that *all three* were of the aberrant hue.[16]

As regards differences relating to the measurable parts, certain preliminary explanations are necessary. It was early found that the cage-born mice depart from the wild type in certain rather striking respects. They are, on the average, considerably smaller than the latter, and have tails, feet and ears which are shorter not only absolutely but relatively. In extreme cases these malformations may fitly be termed deformities. Not rarely, too, the dorsal tail-stripe becomes so diffuse that definite outlines can no longer be distinguished. Measurements reveal the fact that this stripe becomes narrower, on the average, in the cage-born animals. Furthermore, the fertility of the captive generations is greatly reduced.

These abnormal characteristics resulting from captivity are manifested much more strongly by the Eureka race than by the desert one, or by the race which is native to this locality (La Jolla). In fact, my original stock of *rubidus*, consisting of over a hundred animals of the wild generation, has dwindled down to one male and six females in the C_3 generation. In contrast to this, no difficulty has been found in maintaining approximately the original numbers of the other two races, despite the sterility of a large proportion of the individuals. Here, then, we may note in passing, is another interesting racial difference of a physiological nature.

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[15] I there neglected to point out the analogy between this race and that described by Bangs (see Osgood, 1909, p. 121) from the island of Monomoy, Massachusetts. Castle and Phillips, as I learn from Dr. Castle, have bred this form in the laboratory and found its peculiarities to be "really genetic." Morgan's findings (1911) in respect to this question appear to have been complicated by the appearance of artificially induced abnormalities.

[16] In my earlier statement, based upon the appearance of the living animals, it was said that two of the three were exceptionally pale.

This deterioration of the stock, it must be pointed out, is progressive. Each generation probably presents more abnormalities than the preceding one. The causes of this condition are at present entirely unknown to me. Malnutrition or intoxication, resulting from pathogenic bacteria or protozoa in the alimentary canal, may be mentioned as possibilities. Many of the animals are now being reared in small open pens, where they are allowed to burrow in the ground. A preliminary test of this plan encourages us to hope that the troubles referred to may thus be avoided.

The following table presents mean values for certain characters in the C_2 generation, for the three races which are now being reared at La Jolla.

TABLE V

	Sex	No. of Cases	Body (Mm.)	Tail (Per Cent.)	Foot (Mm.)	Ear (Mm.)	Tail-Stripe (Per Cent.)
Eureka	♂	21	85.5	93.1	20.26	16.39	37.3
	♀	13	87.2	91.5	20.30	16.90	39.5
La Jolla	♂	61	87.4	79.6	19.62	17.66	30.7
	♀	43	89.4	79.1	19.56	17.74	31.1
Victorville	♂	45	85.3	75.6	18.65	16.43	25.9
	♀	49	87.0	74.8	18.81	16.90	26.2

It is plain from this table that, in respect to the four characters other than body length (tail length, foot length, ear length and tail-stripe), the three races have maintained the same relative positions in the series as formerly. When arranged with reference to tail, foot and tail-stripe, the series, as before, is: Eureka > La Jolla > Victorville. As regards ear length, the earlier arrangement likewise holds, viz.:

$$\text{La Jolla} > \begin{cases} \text{Eureka,} \\ \text{Victorville.} \end{cases}$$

Another significant fact does not appear from the foregoing table, however. The modifications of the three races, indicated by the consistent reduction of all these values, has not affected them to an equal degree. In respect to all four of the characters (body length not here considered) the local (La Jolla) race has been least modified, while in respect to three of them (tail length, tail-stripe and ear) the Eureka race has been most modified. Thus there has been a mean reduction of 11 per cent. in the tail length of *rubidus,* 7½ per cent. in that of *sonoriensis,* and only 5 per cent. in that of *gambeli.* There is, therefore, a convergence between the Eureka and the La Jolla races, and if I had only these two under comparison, I might have been disposed to conclude that local conditions had brought about a modification of *rubidus* in the direction of *gambeli.* But the case of *sonoriensis,* which actually diverges farther from the local race in the C_2 than in the parent generation, shows that this explanation is not the correct one. These differences in the degree of modification are probably indices of the susceptibility of these three races to the malign influences of captivity, which have already been discussed. In harmony with this view is the fact that the Eureka mice are likewise far less fertile, under local conditions, than either of the other races.

V. Heredity of Individual Differences within Each Race

It has been shown that a wide range of individual variability occurs within each race in respect to just those characters by which one of these groups is distinguished from another. These major differences which distinguish one race from another have been shown to be hereditary. Is this likewise true of those minor differences which distinguish one individual from another of the same race?

This question can be answered by the well-known method of computing coefficients of parental-filial correlation—the "coefficients of heredity" of Pearson. I realize that the validity of this measure of the force of heredity has been called in question,[17] on the ground that it does nothing more than reveal the presence of genetically different strains in a mixed population. This, however, is exactly what I wish to do in the present case. The fact that within a "pure line," where the phenomena of heredity should be least obscured, this coefficient is said to be zero is entirely irrelevant to the present situation. What we wish to ascertain is the degree to which, for example, long-tailed parents tend to have long-tailed offspring. Whether these differences among the parents are due to "mutations" or "fluctuating variations," whether they are due to single "unit factors" or "multiple factors" or no factors at all, are admittedly matters upon which these coefficients throw no light. Such questions must be decided upon other grounds.[18]

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[17] By Pearl (1911) and Johannsen (1913), among others.

In computing these correlations between parents and offspring, we are restricted to characters which are independent of the absolute size of the individual.[19] Characters which fulfil these requirements fairly well are the *relative* tail length (ratio to body) and the relative width of the tail-stripe (ratio to circumference). My data show that the former is largely, and the latter almost wholly, independent of the size of the mouse.

The coefficients are given in Table VI. I have not thought it worth while to include their probable errors, since the significance of the set as a whole is indicated by the magnitude of most of the figures and by the fact that all but two out of the 24 are positive. The weighted means of these coefficients, combining the four races and two sexes, are: relative tail length, +0.297; tail-stripe,

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[18] One objection, valid in certain cases, has been raised against the use of this coefficient. I refer to the contention that it may reveal resemblances which are due not to genetic relationship, but to environmental influences which are similar for parent and offspring, while dissimilar for distinct descent lines. If any one is disposed to raise this objection in the present case, it is sufficient to reply that all of my parent animals of a given race were trapped in the same restricted area, while all the offspring were reared in captivity under conditions which were practically identical for all.

[19] Unless size, itself, were to be taken as the character in question. The absolute length of the tail or foot, on the other hand, is not available for such computations. The progeny of long-tailed parents might have relatively long tails, which might, none the less, be absolutely short, owing to the small size of the individuals in question.

TABLE VI

	rubidus		*gambeli* (La Jolla)		*sonoriensis*	
	Tail	Tail-Stripe	Tail	Tail-Stripe	Tail	Tail-Stripe
Father-son	+0.36	+0.08	+0.15	+0.36	+0.23	+0.26
Father-daughter	+0.24	+0.27	+0.11	+0.53	+0.42	+0.17
Mother-son	+0.64	+0.57	+0.51	+0.36	+0.28	+0.26
Mother-daughter	+0.84	+0.47	−0.02	+0.51	+0.15	−0.02

+ 0.302. The average of four figures given by Pearson[20] (father-son, father-daughter, etc.) for the heredity of stature in man is + 0.335. There is thus found, in these mice, approximately the same degree of resemblance between parents and offspring, in respect to these two characters, as is found to occur in man in respect to stature.[21]

Since the heritability of these individual differences has been proven by means of correlation coefficients, the practicability of selection experiments with such characters is evident, provided that sufficient numbers of normal animals can be reared. Experiments of this nature have already been commenced by Mr. H. H. Collins and myself. The characters chosen for these tests are coat color, tail length and width of tail stripe.

VI. Hybridization

Successful hybrid matings have been made (1) between the Berkeley and the Victorville mice, (2) between the Eureka and the La Jolla mice, and (3) between the Eureka and the Victorville mice.

In the first case, moderate numbers of F_1 and F_2 animals were reared. In respect to coat color, the 25 F_1 individuals, when adult, ranged from a condition similar to that of an average Berkeley *gambeli* to a condition as pale and as yellow as that of the average *sonoriensis*. Moreover, there was here no marked tendency for the mean or intermediate condition to preponderate numerically over the extremes.

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[20] 1900, p. 458.

[21] It is likely that the abnormal condition of the cage-born mice, described above, has resulted in minimizing this correlation. Some of the differences among them are doubtless due, not to heredity, but to differences in the incidence of the disturbing factor (infection?). The parents, having grown nearly or quite to maturity in the wild state, were not subjected to this influence.

Now it is of interest to note that the F_2 generation, consisting of 40 specimens, presented very nearly the same range, in respect to coat color, as did the F_1. The two dark extremes were of an almost identical shade, as were likewise the pale extremes.[22] No argument for "segregation" could be based upon this series which would not apply with equal force to the F_1 series.

Twenty F_3 mice, resulting from random matings of the F_2 animals, presented a range of variation which was actually not as great as that observed in the F_2 generation. The smaller number may perhaps be responsible for this difference.

It must be added that both of the parent races present a rather wide range of variability as regards coat color, and that series of the two overlap rather broadly in this respect. This circumstance complicates our interpretations much more in the present case than in that of the crosses between *rubidus* and *sonoriensis,* which will be considered later.

The Berkeley and Victorville races have been found to differ in only two of the characters which were subjected to careful measurement. The former race has a broader dorsal tail-stripe and slightly shorter ears. The second of these differences is a trifling one, however, and is not always evident when small series are compared. Moreover, the absolute length of the ear is largely dependent upon the size of the body.

Thus the width of the tail-stripe is the only accurately measured subspecific character which is available in considering hybrids between these two races. Table VII gives the mean value and the variability of this character in the two parent races[23] and in the F_1 and F_2 generations of hybrids.

Despite the small numbers of animals here concerned, two facts are of some interest. (1) The mean width of the tail-stripe in both generations of hybrids is very nearly midway between the mean widths found in the parent races. (2) There is no increase in the variability

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[22] These remarks are based upon a comparison of skins, after death.

[23] The parent mice here used were cage-born animals, which, as before stated, were somewhat modified by captivity. They represent the limited stock which was reared in Berkeley during the earlier stages of the experiment.

TABLE VII

	Number of Animals Measured	Mean	Standard Deviation
gambeli (Berkeley)	23	33.5	4.09
sonoriensis	38	26.5	4.57
F_1 hybrids	24	30.2	3.96
F_2 hybrids	38	29.3	3.54

of this character in the F_2 generation. Indeed, the standard deviation for the latter animals chances to be the lowest of the four values given.

It seems worth while to indicate the actual distribution frequencies of the tail-stripe measurements for these four groups of mice (Table VIII).

TABLE VIII

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Average
Berkeley *gambeli* ...					1				1	1	1		3	2	3		2	2	4	1	1	1	33.5
sonoriensis ..	2	2	2	3	2	4	2	2	2	4	3	2	2	1	1	2	2						26.5
F_1 hybrids...		1				1		1	3	1	4	2	1	4	1	2	2				1		30.2
F_2 hybrids...				1	1	1	3	3	4	2	6	2	3	3	3	4	1	1					29.3

In contrast to this case of the tail-stripe, it is interesting to note that, in respect to relative tail length, the F_2 generation shows a somewhat higher variability than the F_1 generation or than either of the parent races. But it so happens that this is a character *in which the parent races do not appreciably differ.*

In reality, it is probable that none of these differences in variability is significant, in view of the small numbers of individuals concerned. The explanation offered for certain differences between other hybrids to be discussed later—namely, that the F_1 and F_2 generations differed in the relative degree of abnormality—does not seem to apply here. The mean body length is about equal in the two generations, as well as the mean length of tail and foot.

The crosses between the Eureka and the La Jolla races have not been carried far enough to render any report upon them possible at present.

Hybridization of the Eureka with the desert mice was first accomplished nearly two years ago, and thus far 30 F_1 and 20 F_2 animals have been reared to maturity and measured. A very serious drawback has been the great infertility, under local conditions, of *rubidus* and anything having *rubidus* "blood." Still more serious is the abnormal state of a large proportion of the cage-born animals, which affects some of the very parts that we are chiefly concerned with in these crosses. Fortunately, the coat color remains nearly, or quite unaltered.

My series of 30 F_1 skins, taken as a whole, presents a condition about intermediate between that of the parent races. They exhibit, however, a wide range of variation, the darkest individuals being nearly as dark as some of the palest wild specimens of the Eureka race, while the palest individuals differ little in shade from a medium mouse of the desert race (Fig. 13).

In the F_2 generation we meet with a range which is little, if any, greater. The darkest skin[24] is somewhat darker than the darkest in the F_1 generation. On the other hand, the palest skin is scarcely as pale as the palest in the F_1. The preponderating effect is that the hybrids of the second generation, like those of the first, are *intermediates*. If these differences of coat color are conditioned at all by Mendelian "unit factors," there must be more than one pair of allelomorphs concerned. The monohybrid ratio is obviously lacking, and there is no segregation into distinguishable classes. Furthermore, it must be borne in mind that no indirect evidence for segregation can be pointed out in the F_2 generation which is not equally manifested in the F_1.

TABLE IX[24]

	No. of Animals	Body (Mm.)	Tail (Per Cent.)		Foot (Mm.)		Tail-Stripe (Per Cent.)	
		Mean	Mean	S. D.	Mean	S. D.	Mean	S. D.
rubidus (cage-born) ..	61	87.80	98.5		20.82		38.3	
sonoriensis (cage-born)	121	86.48	78.4		19.22		24.7	
F_1 hybrids...........	21	86.43	88.0	4.3	20.09	0.85	31.3	4.0
F_2 hybrids...........	20	84.70	84.3	6.9	19.45	1.12	33.6	6.5

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[24] This happens to be a badly shrunken skin, which perhaps does not reveal the original color. The next darkest (shown in the photograph) is of almost exactly the same shade as the darkest F_1 skin.

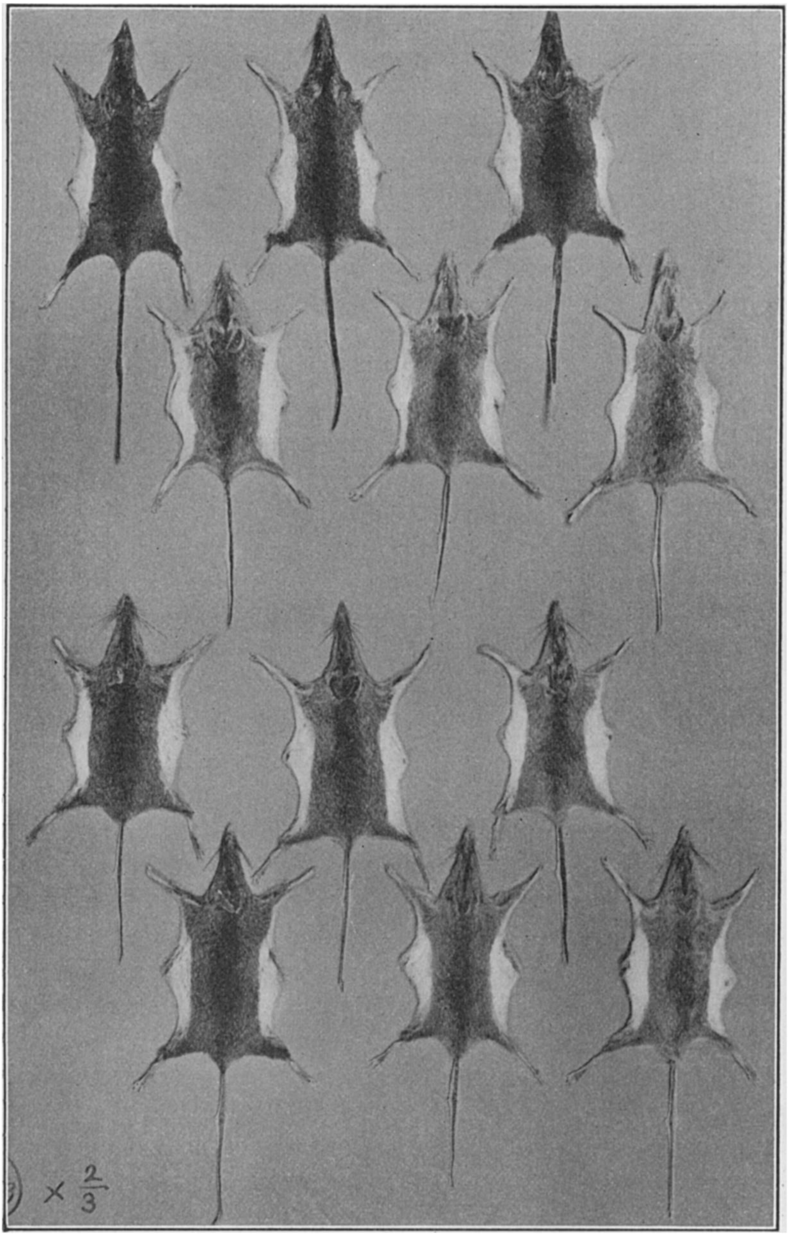

FIG. 13. Skins of pale, intermediate and dark individuals of *P. m. rubidus* (first line), of *P. m. sonoriensis* (second line), and of F_1 and F_2 hybrids between these races (third and fourth lines).

As regards the measurable characters which differentiate the parent races, some light upon their behavior in hybridization may be derived from the data in Table IX. Here, too, one fact seems plain, despite the small number of individuals, and the modifications which these mice share with cage-born mice in general. This is the intermediate condition of the hybrids, both F_1 and F_2, as regards tail length, foot length and tail-stripe. The ear measurements have not been introduced into these comparisons, since the parent races do not differ in this respect.

As regards variability, it is seen that the standard deviations of the F_2 generation are all three larger than those of the F_1, and the differences seem great enough to be of possible statistical significance. I have, however, tabulated the frequencies of the various values for these three characters (not reproduced here), and I find that the probable explanation of this increase of variability in the F_2 generation is an increase in the amount of abnormality in the latter. This is to be inferred from the fact that the extension in range is chiefly in the direction of the *lower* values, while in two of the three cases the uppermost figures actually fall below those of the F_1. Now the abnormal influences of captivity operate by decreasing (oftentimes considerably) the values for these very characters. As further evidence for this interpretation is the fact that the average body size of the F_2 mice is here less than that of the preceding generation.

A considerable number of back crosses have been obtained between each of the hybrid combinations above discussed and one or both of the parent races. The number of individuals in any one series is, however, small, so that it is hardly worth while to deal with the results of these crosses here. They afford as little evidence of complete segregation of the subspecific color types as do the hybrids previously considered.

(*To be concluded*)

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[25] Standard deviations for the parent races have been computed only for the two sexes separately. They are, therefore, not included in this table. Nine of the 30 F_1 animals are not here included, since the *rubidus* parents of these were caught at some distance from Eureka.